Climate niche conservatism does not explain restricted distribution patterns in *Tynanthus* (Bignonieae, Bignoniaceae)

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Studies on niche evolution allow us to establish how species niches have changed over time and to identify how long-term evolutionary processes have led to present-day species distributions. Here, we investigate the patterns of climatic niche evolution in *Tynanthus* (Bignonieae, Bignoniaceae), a genus of narrowly distributed species. We test the hypothesis that niche conservatism has played an important role in the history of this group of Neotropical lianas. We perform univariate and multivariate comparisons between climatic niches of species and associated environmental data with information on phylogenetic relationships. We encountered considerable divergence in niches among species, indicating that niche conservatism in climatic variables does not seem to have played a key role in the history of the genus. © 2015 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2015, **179**, 95–109.

ADDITIONAL KEYWORDS: lianas – Neotropical flora – niche evolution – niche overlap – species distribution patterns.

INTRODUCTION

The factors determining species distribution patterns in space and time have long intrigued ecologists and biogeographers (Brown, Stevens & Kaufman, 1996). It is now clear that species ranges are determined by a set of abiotic and biotic conditions (e.g. available climate) that are known as a species niche (Hutchinson, 1957) which, with historical factors, seem to have shaped present-day distribution patterns. In this context, it is critical that analyses of niche elements of multiple species incorporate information on the phylogenetic history of the focal taxa so that a complete picture of the factors shaping species distributions can be achieved (e.g. Rice, Martínez-

Meyer & Peterson, 2003; Knouft *et al.*, 2006; Eaton, Soberón & Peterson, 2008; Kozak & Wiens, 2010; Emery *et al.*, 2012; Nyári & Reddy, 2013). Niche studies based on robust phylogenetic frameworks allow us to identify how long-term evolutionary processes have led to present-day distribution patterns, as well as to establish how species niches have changed over time (Wiens, 2011).

Several studies on niche evolution have shown that the ecological requirements of lineages are often conserved over time, with closely related species maintaining their ancestral niche traits and often being more ecologically similar than expected on the basis of their phylogenetic relationships; this pattern is known as niche conservatism (see Wiens *et al.*, 2010). Nevertheless, niche conservatism is not the rule for all organisms and other studies have encountered substantial evidence for niche shifts (i.e. niche overdisper-

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sion) over time (Losos, 2008; Pearman *et al*., 2008; Wiens, 2011). Despite the great breadth of studies on niche evolution, the prevalence of niche conservatism or niche overdispersion remains to be investigated for most groups of organisms.

A better understanding of the level of evolutionary lability of ecological features is critical for a clear understanding of community structure (e.g. Vamosi *et al*., 2009) and species distribution patterns in tropical vs. temperate regions (e.g. Jansson, Rodríguez-Castañeda & Harding, 2013). It also allows for a better evaluation of the resilience of species under climate change (e.g. Wiens *et al*., 2009) and biological invasions (e.g. Petitpierre *et al*., 2012), among others (reviewed by Wiens & Graham, 2005; Pearman *et al*., 2008; Wiens *et al*., 2010; Peterson, 2011; Guisan *et al*., 2014). However, studies of Neotropical plant clades based on robust phylogenetic analyses and a detailed understanding of species niche preferences are still lacking, preventing a complete understanding of factors that have shaped current distribution patterns in the Neotropics (Hughes, Pennington & Antonelli, 2013).

Tynanthus Miers (Bignonieae, Bignoniaceae) is a genus of lianas that is widely distributed in tropical South and Central America (Lohmann & Taylor, 2014; Medeiros & Lohmann, 2015a). *Tynanthus* spp. generally have restricted geographical distribution patterns, occurring predominantly in humid forests from southern Mexico to southern Brazil (Medeiros & Lohmann, 2015a). A taxonomic revision (Medeiros & Lohmann, 2015a) and a robust time-calibrated phylogenetic tree of the genus based on plastid and nuclear markers were used as the basis for a biogeographical study of *Tynanthus* (Medeiros & Lohmann, 2015b). This study indicated that the genus originated between 9.4 and 21.5 Mya, most probably at *c*. 15.3 Mya from an ancestor that was broadly distributed throughout lowland Amazonia, western South America and Central America. It further indicated that closely related *Tynanthus* spp. occupy the same biogeographical region, suggesting that ecological niche features might be conserved in the genus, and may have prevented species from expanding their ranges inside and outside the individual biogeographical regions (Medeiros & Lohmann, 2015b).

In this study, we test the hypothesis that niche conservatism has played a major role in the diversification history of *Tynanthus*. To test this hypothesis, we use climatic variables and occurrence data to estimate the realized ecological niche of the individual species and a robust phylogenetic framework to investigate patterns of climatic niche differentiation in the genus.

MATERIAL AND METHODS

DISTRIBUTION AND CLIMATIC DATA

A comprehensive dataset, including 1780 georeferenced records of 647 unique localities, was assembled from herbarium vouchers for 13 of the 14 currently recognized *Tynanthus* spp. (Medeiros & Lohmann, 2015a); only *T. espiritosantensis* M.C.Medeiros & L.G.Lohmann was excluded because of the small number of collection records. The number of unique localities for each species ranged from five (*T. macranthus* L.O.Williams) to 193 [*T. polyanthus* (Bureau) Sandwith], representing the known distribution of the species well; the exact number of localities per taxon is presented in Appendix 1. This dataset includes the geographical locations and coordinates included in the specimen labels by collectors. When geographical coordinates were not available, these were georeferenced using the Global Gazetteer Version 2.2 (http://www.fallingrain.com/world/index.html) and the database of the Instituto Brasileiro de Geografia e Estatística (http://www.ibge.gov.br/). All records were checked using QGIS 2.0.1 (QGIS Development Team; available at http://qgis.osgeo.org/).

We used the 19 bioclimatic variables from the WorldClim dataset (Hijmans *et al*., 2005) at 2.5 arc-min resolution (roughly 5 km^2). All variables were examined for pairwise correlations using Bioestat 5.3 (Instituto Mamirauá; available at http://www.mamiraua.org.br/) and calculations were conducted based on the values extracted from sampling points throughout the study area, which was determined by a minimum convex polygon enclosing all species records in QGIS (Fig. 1). This analysis led to the selection of six not strongly correlated variables (Spearman's correlation < 0.7) that best reflect the climatic tolerances for *Tynanthus* spp.: 'temperature seasonality' (bio4), 'maximum temperature of the warmest month' (bio5), 'minimum temperature of the coldest month' (bio6), 'precipitation seasonality' (bio15), 'precipitation of the warmest quarter' (bio18) and 'precipitation of the coldest quarter' (bio19).

NICHE QUANTIFICATION AND COMPARISON

Species pairwise comparisons were conducted for the six climatic variables separately. For this comparison, climatic values for the localities of known occurrence of all species were sampled in QGIS and compared through Kruskal–Wallis and subsequent Dunn tests in Bioestat 5.3 (Instituto Mamirauá; available at http://www.mamiraua.org.br/). Species density plots were then produced with package sm 5.4 (Bowman & Azzalini, 2014) in R 3.0.3 (R Core Team; available at http://www.r-project.org/) to visualize the distribution of the individual species data for each variable.
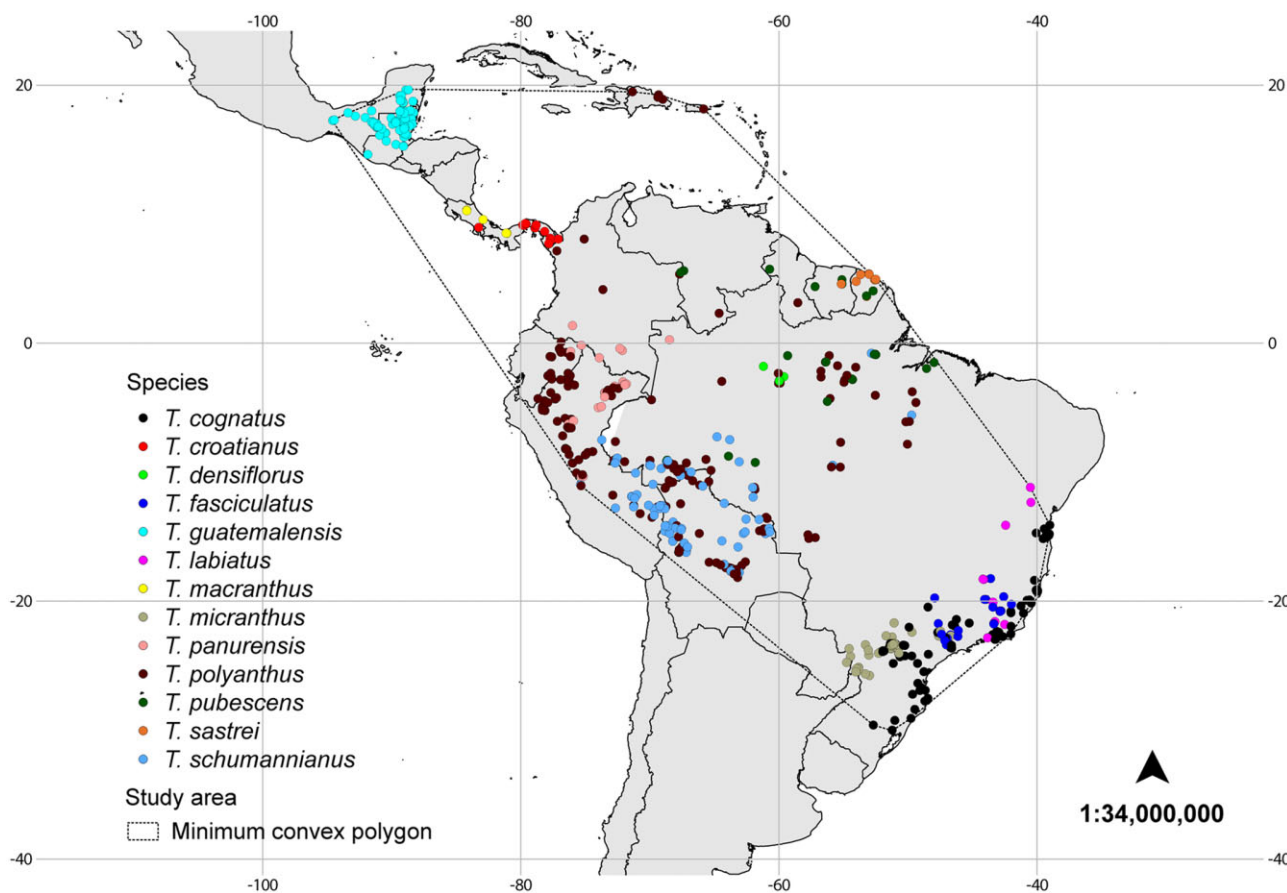
Figure 1. Map showing the boundaries of the study area and the distribution of the 13 *Tynanthus* spp. used for the niche quantifications and comparisons.

We then conducted a multivariate comparison between all species pairs. In these comparisons, niche overlap between taxa was quantified using the PCA-env approach proposed by Broennimann *et al*. (2012) using the functions now available in the ecospat package in R. We used the first two axes of the principal component analysis (PCA) calibrated on the entire climatic space of the study area that includes all the species occurrences (PCA-env in Broennimann *et al*., 2012). The climatic space delimited by the axes was set to 100×100 cells, and niche overlap was estimated using Schoener's *D* metric (Schoener, 1970; Broennimann *et al*., 2012). Statistical tests of niche equivalency and similarity were performed (Warren, Glor & Turelli, 2008). The niche equivalency test evaluates whether the observed overlap between two taxa stays constant when randomly reallocating the species occurrences (i.e. niches of the two species are identical). The niche similarity test assesses how well the occurrence of one species predicts the occurrence of another species by comparing the observed overlap with the overlap observed between the niche of one species and niches randomly selected in the environ-mental space occupied by the other species (i.e. niches of the two species are more similar than expected by chance) (Warren *et al*., 2008; Broennimann *et al*., 2012). Equivalency and similarity tests were performed using 100 replicates.

RECONSTRUCTION OF ANCESTRAL CLIMATIC VARIABLES

We assessed the evolution of the individual climatic variables through ancestral state reconstructions using the R package Phytools 0.3-93 (Revell, 2012). We calculated the mean value for each of the six variables per species and conducted ancestral state reconstructions for continuous characters. A Brownian model of evolution was selected as a better fit, according to the comparison with the Ornstein–Uhlenbeck model conducted with Geiger package for R (Harmon *et al*., 2008). We used the Bayesian tree of *Tynanthus* derived from the combined analysis of nuclear (*pepC*) and plastid (*ndhF* and *rpl32-trnL*) markers (Medeiros & Lohmann, 2015b). The phylogenetic hypothesis is a consensus chronogram that

included one individual of 12 of the 14 recognized *Tynanthus* spp.; only *T. espiritosantensis* (for which we did not have sufficient occurrence records) and *T. sastrei* A.H.Gentry (for which we did not have all DNA sequences) were excluded from this analysis. Parameters for phylogeny estimation follow Medeiros & Lohmann (2015b).

RELATIONSHIP BETWEEN PHYLOGENETIC DISTANCE AND NICHE OVERLAP

We used a Mantel test to check for correlations between climatic niche overlap and phylogenetic distance in *Tynanthus*. For this analysis, we used the matrix of overlap based on Schoener's *D* metric and patristic distances for all species pairs. All analyses were conducted in the R package Vegan 2.0–10 (Oksanen *et al.*, 2013).

RESULTS

UNIVARIATE COMPARISONS

The Kruskal–Wallis test ($P < 0.0001$) supported significant differences among *Tynanthus* spp. with regard to all six climatic variables. The subsequent Dunn tests determined the significant interspecies differences for each variable (Appendix 2). 'Temperature seasonality' (bio4), 'minimum temperature of the coldest month' (bio6) and 'precipitation of the coldest quarter' (bio19) presented more significant than non-significant results (44, 48 and 52 of the 78 pairwise comparisons, respectively; $P < 0.05$), indicating remarkable differences among species niches in these climatic features. The reverse occurred with the 'maximum temperature of the warmest month' (bio5), 'precipitation seasonality' (bio15) and 'precipitation of the warmest quarter' (bio18), all of which presented more non-significant (50, 46 and 49, respectively) than significant results, indicating that these variables are less important for climatic niche differentiation in the genus.

Density plots illustrate the results from the statistical tests (Fig. 2). In the bio4 plot, for example, it is possible to visualize that *T. croatianus* A.H.Gentry, *T. densiflorus* M.C.Medeiros & L.G.Lohmann, *T. macranthus*, *T. panurensis* (Bureau) Sandwith, *T. polyanthus*, *T. pubescens* A.H.Gentry and *T. sastrei* occur predominantly in areas with low temperature seasonality, whereas the remaining species [*T. cognatus* (Cham.) Miers, *T. fasciculatus* (Vell.) Miers, *T. guatemalensis* Donn. Sm., *T. labiatus* (Cham.) Miers, *T. micranthus* Corr. Mello ex K.Schum. and *T. schumannianus* (Kuntze) A.H.Gentry] occur predominantly in areas with higher temperature seasonality. The bio6 plot shows that *T. cognatus*, *T. fasciculatus* and *T. micranthus* occur at higher density in areas with lower minimum temperature of the coldest month than *T. guatemalensis*, *T. labiatus*, *T. macranthus*, *T. polyanthus* and *T. schumannianus*, which, in turn, present lower values of minimum temperature than *T. croatianus*, *T. densiflorus*, *T. panurensis*, *T. pubescens* and *T. sastrei*. The bio19 plot indicates that *T. cognatus*, *T. fasciculatus*, *T. guatemalensis*, *T. labiatus*, *T. micranthus*, *T. polyanthus* and *T. schumannianus* are mainly distributed in areas with lower precipitation in the coldest quarter than *T. croatianus*, *T. densiflorus*, *T. macranthus*, *T. panurensis*, *T. pubescens* and *T. sastrei*. The bio5, bio15 and bio18 plots, however, do not show any clear pattern of variation in climatic features among species groups. These plots generally show a high overlap of the diverse curve shapes.

MULTIVARIATE COMPARISONS

The PCA based on the climatic space of the study area returned two axes that together explain 66.80% of the total variation (PC1 = 39.36% and PC2 = 27.44%). The contribution of each variable to both axes and the climatic space occupied by each species are presented in Figure 3. The climatic variables highlighted by the density plots as the most important are those associated with PC1 (bio4, bio6). Pairwise overlap ranged from $D = 0$ to $D = 0.618$ (Fig. 4; Appendix 3). Overlap is low in most cases, with 47 comparisons (around 60% of the total) returning $D < 0.1$. Six of the nine highest values ($D > 0.3$) were obtained for species pairs whose distributions are partially coincident or adjacent (*T. cognatus–T. fasciculatus*, *T. cognatus–T. micranthus*, *T. fasciculatus–T. micranthus*, *T. macranthus–T. polyanthus*, *T. polyanthus–T. pubescens* and *T. polyanthus–T. schumannianus*).

NICHE EQUIVALENCY AND SIMILARITY TESTS

The hypothesis of niche equivalency between species pairs was rejected in every case ($P < 0.02$), indicating that no pair of species is climatically identical. In the niche similarity tests, most species pairs showed an overlap that falls within the 95% confidence interval of the null distribution. Only in four instances was a two-way significant niche similarity obtained (*T. cognatus–T. fasciculatus*, *T. cognatus–T. micranthus*, *T. guatemalensis–T. schumannianus* and *T. macranthus–T. polyanthus*), indicating that climatic niches were more similar than expected by chance. One-way significant similarity was obtained for *T. fasciculatus–T. labiatus*, *T. fasciculatus–T. macranthus* and *T. polyanthus–T. pubescens*.

ANCESTRAL CLIMATIC NICHE RECONSTRUCTIONS

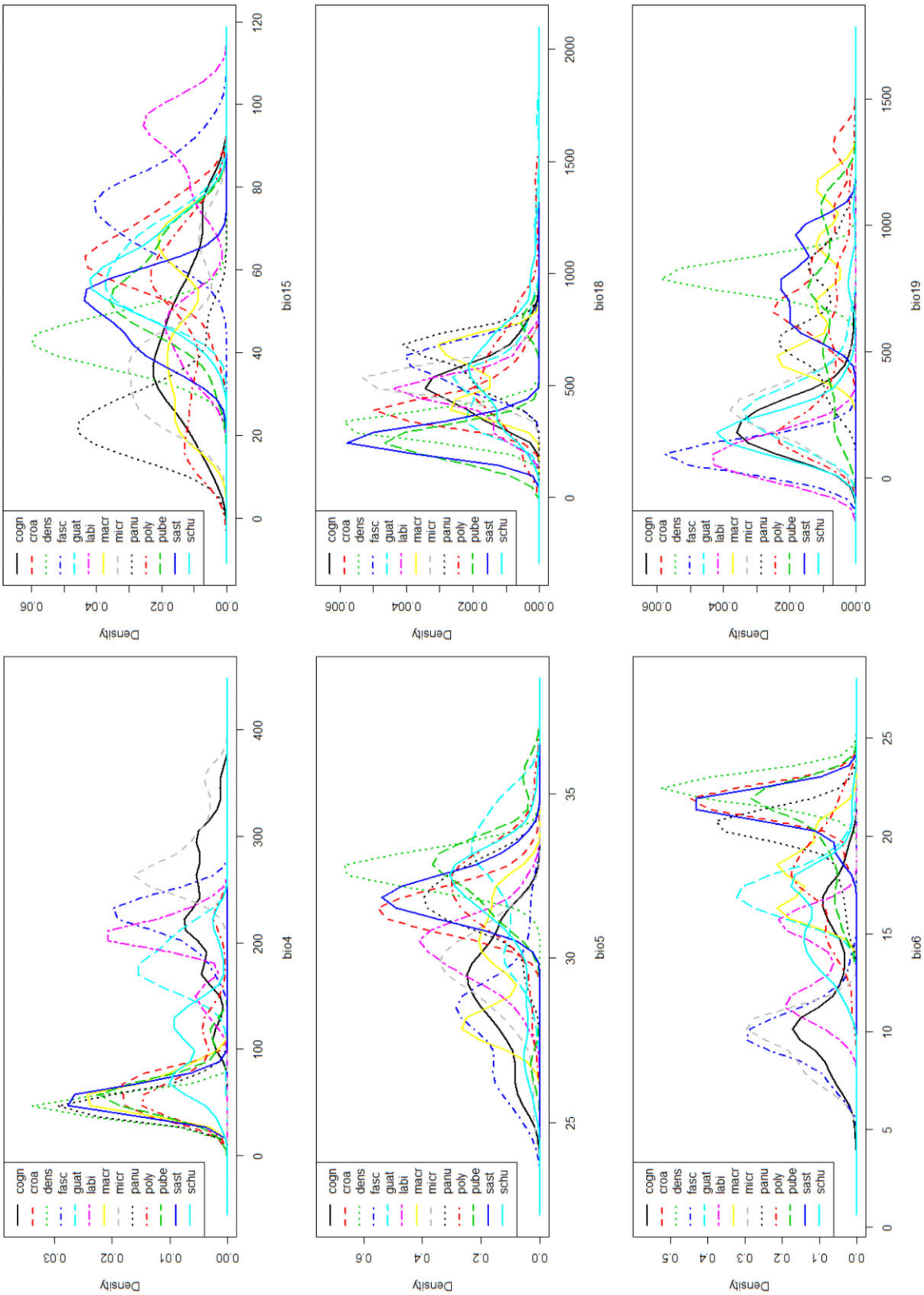The observed and estimated mean values for each of the six climatic variables are represented by a colour

Figure 2. Density plots of the six climatic variables for the 13 *Tynanthus* spp. analysed. bio4, temperature seasonality; bio5, maximum temperature of the warmest month; bio6, minimum temperature of the coldest month; bio15, precipitation seasonality; bio18, precipitation of the warmest quarter; bio19, precipitation of the coldest quarter. Species names are abbreviated using the four initial letters of the specific epithet.
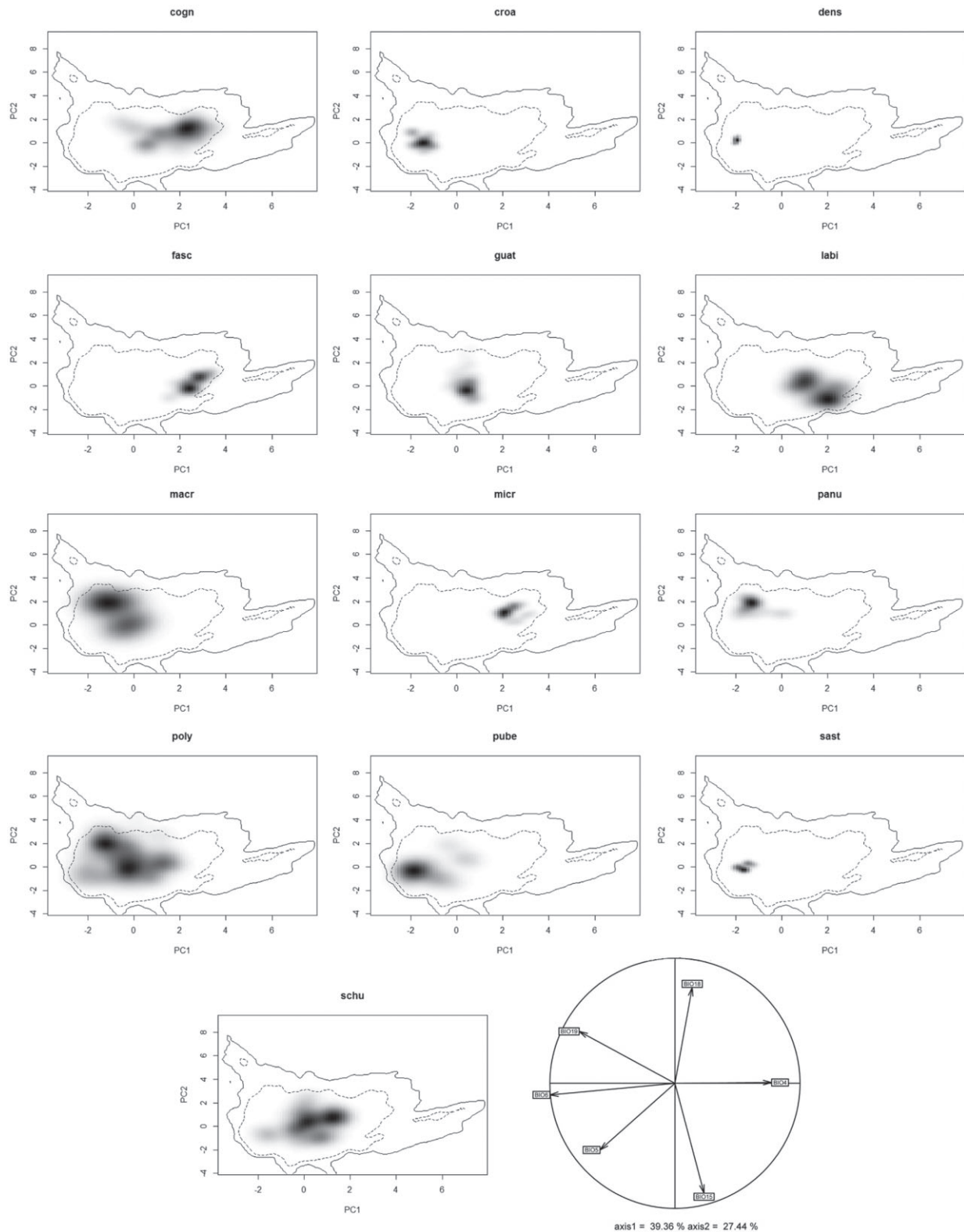
Figure 3. Niches of *Tynanthus* spp. in climatic space delimited by the first two principal component axes. Shading represents the density of occurrences of each species by cell. Solid and broken contour lines show 100% and 50% of the available environment, respectively. The correlation circle illustrates the contribution of the individual climatic variables to the two principal component axes. Species names are abbreviated using the four initial letters of the specific epithet.
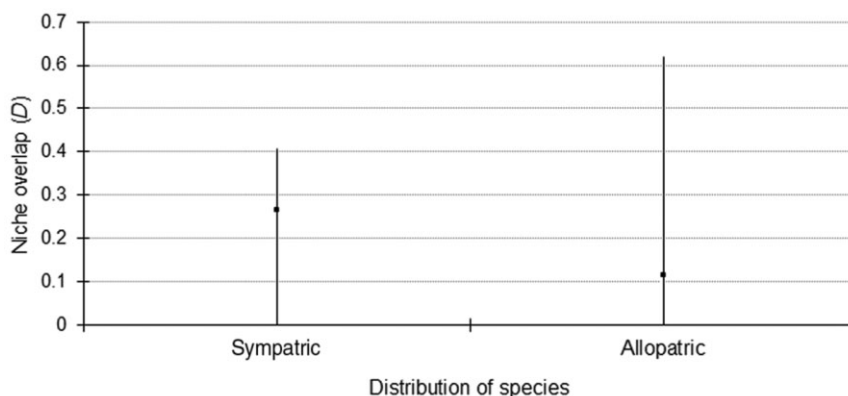
Figure 4. Maximum, minimum and median values of niche overlap (Schoener's *D*) observed in pairwise comparisons for sympatric and allopatric species. Distribution areas considered were Atlantic forest, Amazonia and Central America.

gradient in the simplified phylogenetic tree presented in Figure 5. The ancestral condition for the genus was low to intermediate temperature seasonality (bio4). This condition was lower in the ancestor of the *panurensis* clade, composed of *T. croatianus*, *T. guatemalensis*, *T. densiflorus*, *T. panurensis* and *T. pubescens* (Medeiros & Lohmann, 2015b), and higher in the ancestor of the *T. micranthus* + *T. fasciculatus* + *T. labiatus* clade. Furthermore, the most recent common ancestor (MRCA) of the genus presented an intermediate value for the maximum temperature in the warmest month (bio5). The value of bio5 increased in the *panurensis* + *labiatus* clade (i.e. *T. schumannianus* + *T. micranthus* + *T. fasciculatus* + *T. labiatus*; Medeiros & Lohmann, 2015b) and became even higher in the *panurensis* clade, but decreased in the *labiatus* clade.

For the minimum temperature in the coldest month (bio6), the ancestral condition is intermediate, increasing in the *panurensis* clade, but decreasing in the *T. micranthus* + *T. fasciculatus* + *T. labiatus* subclade. The MRCA of *Tynanthus* occurred in areas with intermediate values of precipitation seasonality (bio15); these values increased in the *T. croatianus* + *T. guatemalensis* subclade and in the ancestor of the *labiatus* clade, with a subsequent increase in the *T. fasciculatus* + *T. labiatus* subclade. The MRCA of *Tynanthus* also occurred in an area with high values of precipitation of the warmest quarter (bio18); intermediate values are observed in the MRCA of the *panurensis* + *labiatus* clade, with a decrease in these values in the *panurensis* clade, and an increase in the *labiatus* clade. Finally, the MRCA of *Tynanthus* occupied an area with intermediate values for the precipitation of the coldest quarter (bio19); this variable increased in the *panurensis* clade and decreased in the *labiatus* clade.

PHYLOGENETIC DISTANCE AND NICHE OVERLAP

Results from the Mantel test indicate a lack of significant correlation between climatic niche overlap and phylogenetic distance in *Tynanthus* ($r = 0.16$; $P = 0.17$). These results are presented in Figure 6.

DISCUSSION

In this study, we investigated the patterns of climatic niche evolution in *Tynanthus* (Bignonieae, Bignoniaceae) and tested the hypothesis that niche conservatism has played a major role in the diversification history of this genus. Comparisons of species climatic niches and associated environmental data with information on phylogenetic relationships among the various species recovered considerable divergence in climatic niches among species. Our results are used as a basis to discuss ecological patterns in the genus and to suggest novel approaches for future analyses.

NICHE EVOLUTION

The analysis of each of the six climatic variables considered indicated that temperature seasonality (bio4), minimum temperature of the coldest month (bio6) and precipitation of the coldest quarter (bio19) account for the majority of the observed differentiation in *Tynanthus*. These results were obtained through the analysis of the overall geographical distribution of each species; therefore, species that inhabit the same biogeographical area have similar climatic niche characteristics. For example, the Atlantic forest species *T. cognatus*, *T. fasciculatus* and *T. micranthus* predominate in areas that are characterized by a higher temperature seasonality, lower minimum temperature of the coldest month and lower precipitation of the coldest quarter than the Amazonian *T. densiflorus*,
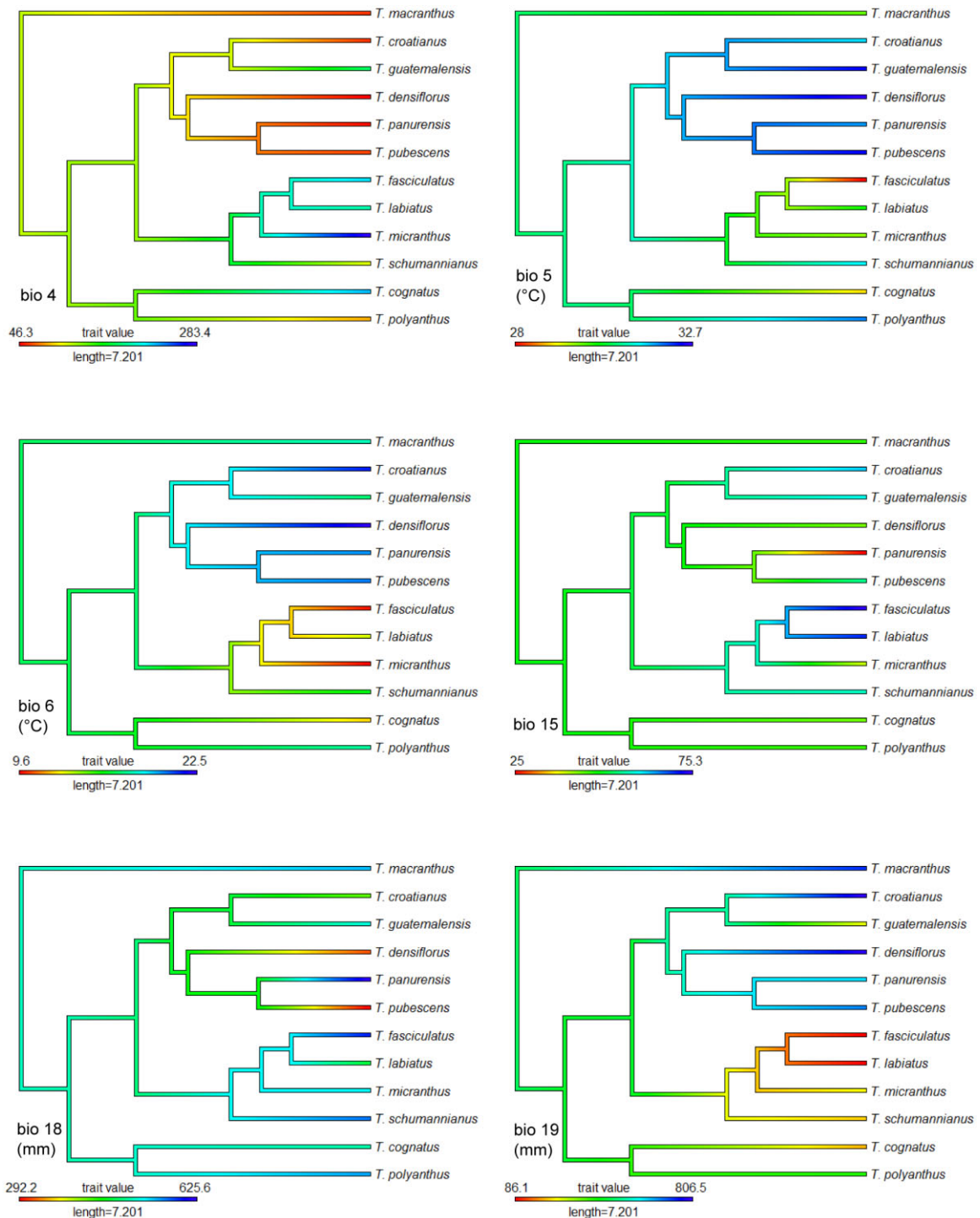
Figure 5. Ancestral character reconstructions of the mean value for the six climatic variables used in the niche quantifications and comparisons. bio4, temperature seasonality; bio5, maximum temperature of the warmest month; bio6, minimum temperature of the coldest month; bio15, precipitation seasonality; bio18, precipitation of the warmest quarter; bio19, precipitation of the coldest quarter.
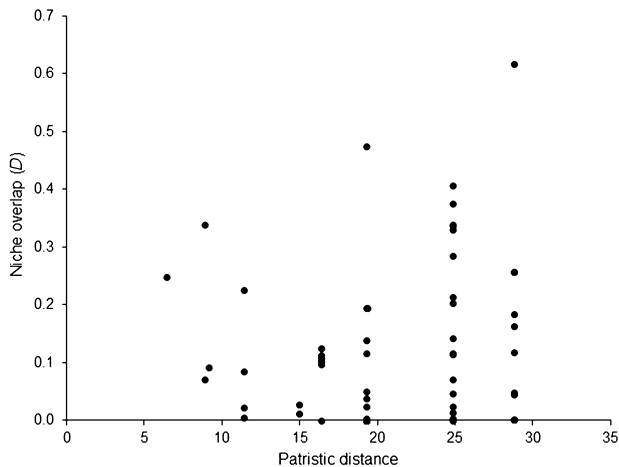
Figure 6. Dispersion diagram illustrating the lack of correlation between the pairwise matrices of climatic niche overlap and patristic distances for the 13 analysed *Tynanthus* spp.

T. panurensis, *T. pubescens* and *T. sastrei*. These observations reflect the typical climatic features of each of the biogeographical regions considered (Peel, Finlayson & McMahon, 2007; Garreaud *et al*., 2009). In other words, the climatic niche variables considered here generally reflect large-scale biogeographical patterns. However, *T. labiatus*, another species from the Atlantic forest, differs from the other Atlantic taxa along the gradient of minimum temperature of the coldest month.

In contrast with temperature seasonality (bio4), temperature of the coldest month (bio6) and precipitation of the coldest quarter (bio19), our results showed that maximum temperature of the warmest month (bio5), precipitation seasonality (bio15) and precipitation of the warmest quarter (bio18) generally provide less information about the climatic niche differences among species of *Tynanthus*. This is because the mean values of these climatic features are not particularly variable in the areas in which most of the *Tynanthus* spp. occur, especially Amazonia and Central America (Peel *et al*., 2007; Garreaud *et al*., 2009).

Although it is possible to visualize some broad climatic affinities among *Tynanthus* spp., the multivariate comparisons indicate that niche overlap is generally low. The overall divergence in climatic features was also shown by the similarity tests, most of which gave non-significant results, especially in the case of taxa that belong to distinct geographical regions (e.g. *T. cognatus–T. sastrei*, $D = 0$, $p_{1,2} = 0.24$, $p_{2,1} = 0.32$; *T. labiatus–T. macranthus*, $D = 0.048$, $p_{1,2} = 0.24$, $p_{2,1} = 0.18$), but also for species that occur in adjacent areas (e.g. *T. croatianus–T. guatemalen-*

sis, $D = 0.004$, $p_{1,2} = 0.77$, $p_{2,1} = 0.97$; *T. labiatus–T. micranthus*, $D = 0.071$, $p_{1,2} = 0.5$, $p_{2,1} = 0.81$) (Fig. 4; Appendix 3).

Many closely related *Tynanthus* spp. also occur in the same biogeographical region (Medeiros & Lohmann, 2015b). Despite this, no significant relationship was found between climatic niche overlap and phylogenetic distance (Mantel test; $r = 0.16$; $P = 0.17$). This result may be an effect of three different processes that may have taken place during the diversification history of the group, individually or concomitantly. First, the allopatric or parapatric speciation events that have probably predominated along the diversification of *Tynanthus* may have prevented close relatives from coexisting locally (Warren *et al*., 2014). For example, we could suggest that the allopatric ranges presented by the closely related *T. densiflorus*, *T. panurensis* and *T. pubescens* in the Amazonian region (see Fig. 1) result directly from the geography of speciation events and justify the observed ecological differences among these species. Second, the closely related species that occur in the same broad biogeographical area may have experienced niche differentiation during their diversification. In this case, it would be reasonable to presume that climatic niche requirements in *Tynanthus* are labile. A similar interpretation has often been used to discuss results from several studies on the niche evolution of different organisms (Losos, 2008; Pearman *et al*., 2008). Third, the observed differentiation may have been determined or influenced by ecological factors other than the climatic ones treated here, especially those more easily detectable at finer spatial scales (Wiens, 2011; Crisp & Cook, 2012). For instance, biotic interactions, such as competition between closely related taxa, might be driving species to different micro-environmental conditions, resulting in niche differences. It is also possible that competition might explain the relatively reduced range size of some *Tynanthus* spp. In other words, ecological specialization may prevent species from expanding their distribution range, especially in the case of sympatric taxa with similar ecological requirements. Further ecological studies aimed at addressing competition among *Tynanthus* spp. would allow for an adequate test of this prediction. In particular, finer scale analyses of traits in relation to a variety of environmental variables, including ecological aspects associated with establishment and survival (e.g. soil conditions, host preference, pollinators) (Bazzaz, 1991; Schnitzer & Bongers, 2002), would further clarify which ecological aspects may lead to competition among species. In the tribe Bignonieae, in general, competition for pollinators seems to have had minor effects on community assembly (Alcantara *et al*., 2014). However, this hypothesis

should be further tested in other clades of Bignonieae with complete phylogenetic sampling, such as *Tynanthus*.

Overall, our reconstructions of climatic features indicated that the climatic characteristics of the habitat inhabited by the MRCA of *Tynanthus* were predominantly intermediate, as expected for reconstructions based on the Brownian model of evolution, except for the low temperature seasonality and high precipitation of the warmest quarter. Changes that occurred during the diversification history of *Tynanthus* probably led to the establishment of the climatic conditions currently occupied by *Tynanthus* spp. These results received further support from univariate comparisons, and mainly reflected the differentiation between Amazonia + Central America and Atlantic forest species. The diversification of *Tynanthus* throughout Amazonia and Central America was marked by a decrease in temperature seasonality and an increase in maximum temperature of the warmest month, minimum temperature of the coldest month and precipitation of the coldest quarter, but the opposite scenario was observed during the diversification of *Tynanthus* throughout the Atlantic forest. No clear pattern was observed with seasonality of precipitation and precipitation of the warmest quarter; however, some exceptions occurred in specific taxa (e.g. *T. guatemalensis* and *T. schumannianus*; Fig. 5).

FINAL REMARKS

Mixed evidence for niche conservatism is available in the literature. The contradictory findings regarding the prevalence of conservation of niche features in different lineages indicate that it should be explicitly examined instead of assumed a priori (Losos, 2008). The recent application of standardized statistical tests for niche conservatism (e.g. Broennimann *et al.*, 2012; Martínez-Cabrera *et al.*, 2012; Ahmadzadeh *et al.*, 2013) has led to a more objective way to test these hypotheses. In our study, initial biogeographical analyses suggested that niche conservatism might be driving species distribution patterns in *Tynanthus* (Medeiros & Lohmann, 2015b). Despite this, the detailed studies on climatic niche evolution conducted here indicated an overall climatic differentiation among closely related species in the genus, rejecting a niche conservatism hypothesis. In other words, the occupation of the same broad biogeographical areas by phylogenetically closely related species (Medeiros & Lohmann, 2015b) may have been determined by factors or processes other than climatic niche conservatism. This hypothesis remains to be tested with more detailed ecological data. These findings high-light the importance of explicitly testing niche conservatism hypotheses instead of assuming niche conservatism a priori.

The unexpected lack of constancy and evolutionary conservation in niche features reported here only applies to the specific climatic variables and scale of this study. Different results might be encountered when other niche aspects are considered (e.g. ecophysiological) and/or if other spatial scales (e.g. population level) are taken into account. Fine-scale analyses of the distribution of sympatric species would be of particular interest, so that habitat use and fine-scale drivers of species distributions could be examined (see Emery *et al.*, 2012).

Studies on the evolutionary pattern of ecological features for Neotropical plant clades are still scarce despite the high levels of diversity encountered in this region. Similar to *Tynanthus*, high climatic niche variability was reported for clades of Poaceae from dry areas of western South America (Jakob *et al.*, 2010). For *Cedrela* (Meliaceae), it was found that both conservatism and differentiation of climatic features have taken place during the diversification of the group (Koecke *et al.*, 2013). Based on these findings and the results presented here, we would presume that variability in the climatic niche of Neotropical plants may have affected the delineation of present-day distribution patterns. Nevertheless, a synthesis and clear understanding of the exact role of ecology for the history of Neotropical taxa will only be achieved once multiple studies, based on a variety of features and taxa, are available.

ACKNOWLEDGEMENTS

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APPENDIX

Appendix 1. Species included in the dataset used for niche quantification and comparison, followed by the number of unique localities

Species	Localities
Tynanthus cognatus (Cham.) Miers	101
Tynanthus croatianus A.H.Gentry	17
Tynanthus densiflorus M.C.Medeiros & L.G.Lohmann	8
Tynanthus fasciculatus (Vell.) Miers	31
Tynanthus guatemalensis Donn. Sm.	93
Tynanthus labiatus (Cham.) Miers	14
Tynanthus macranthus L.O.Williams	5
Tynanthus micranthus Corr. Mello ex K.Schum.	42
Tynanthus panurensis (Bureau) Sandwith	24
Tynanthus polyanthus (Bureau) Sandwith	193
Tynanthus pubescens A.H.Gentry	23
Tynanthus sastrei A.H.Gentry	10
Tynanthus schumannianus (Kuntze) A.H.Gentry	86

Appendix 2. Univariate pairwise comparisons. Significant ($P < 0.05$) and non-significant (n.s.) values of the Dunn tests are indicated. bio4, temperature seasonality; bio5, maximum temperature of the warmest month; bio6, minimum temperature of the coldest month; bio15, precipitation seasonality; bio18, precipitation of the warmest quarter; bio19, precipitation of the coldest quarter. Species names are abbreviated to the four initial letters of the specific epithet

Species pairs	bio4	bio5	bio6	bio15	bio18	bio19
cogn–croa	< 0.05	< 0.05	< 0.05	< 0.05	n.s.	< 0.05
cogn–dens	< 0.05	< 0.05	< 0.05	n.s.	< 0.05	< 0.05
cogn–fasc	n.s.	n.s.	n.s.	< 0.05	< 0.05	< 0.05
cogn–guat	< 0.05	< 0.05	< 0.05	< 0.05	n.s.	n.s.
cogn–labi	n.s.	n.s.	n.s.	< 0.05	n.s.	< 0.05
cogn–macr	< 0.05	n.s.	n.s.	n.s.	n.s.	< 0.05
cogn–micr	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
cogn–panu	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05
cogn–poly	< 0.05	< 0.05	< 0.05	n.s.	n.s.	< 0.05
cogn–pube	< 0.05	< 0.05	< 0.05	n.s.	< 0.05	< 0.05
cogn–sast	< 0.05	< 0.05	< 0.05	n.s.	< 0.05	< 0.05
cogn–schu	< 0.05	< 0.05	< 0.05	< 0.05	n.s.	n.s.
croa–dens	n.s.	n.s.	n.s.	< 0.05	n.s.	n.s.
croa–fasc	< 0.05	< 0.05	< 0.05	n.s.	< 0.05	< 0.05
croa–guat	< 0.05	n.s.	< 0.05	n.s.	n.s.	< 0.05

Appendix 2. *Continued*

Species pairs	bio4	bio5	bio6	bio15	bio18	bio19
croa–labi	< 0.05	n.s.	< 0.05	n.s.	n.s.	< 0.05
croa–macr	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
croa–micr	< 0.05	n.s.	< 0.05	< 0.05	n.s.	< 0.05
croa–panu	n.s.	n.s.	n.s.	< 0.05	< 0.05	n.s.
croa–poly	n.s.	n.s.	< 0.05	< 0.05	n.s.	< 0.05
croa–pube	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
croa–sast	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
croa–schu	n.s.	n.s.	< 0.05	n.s.	< 0.05	< 0.05
dens–fasc	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05
dens–guat	< 0.05	n.s.	< 0.05	n.s.	n.s.	< 0.05
dens–labi	< 0.05	< 0.05	< 0.05	< 0.05	n.s.	< 0.05
dens–macr	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
dens–micr	< 0.05	< 0.05	< 0.05	n.s.	< 0.05	< 0.05
dens–panu	n.s.	n.s.	n.s.	n.s.	< 0.05	n.s.
dens–poly	n.s.	n.s.	< 0.05	n.s.	< 0.05	< 0.05
dens–pube	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
dens–sast	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
dens–schu	n.s.	n.s.	< 0.05	n.s.	< 0.05	< 0.05
fasc–guat	n.s.	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05
fasc–labi	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
fasc–macr	< 0.05	n.s.	< 0.05	< 0.05	n.s.	< 0.05
fasc–micr	n.s.	n.s.	n.s.	< 0.05	n.s.	< 0.05
fasc–panu	< 0.05	< 0.05	< 0.05	< 0.05	n.s.	< 0.05
fasc–poly	< 0.05	< 0.05	< 0.05	< 0.05	n.s.	< 0.05
fasc–pube	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05
fasc–sast	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05
fasc–schu	< 0.05	< 0.05	< 0.05	< 0.05	n.s.	< 0.05
guat–labi	n.s.	< 0.05	< 0.05	n.s.	n.s.	< 0.05
guat–macr	< 0.05	n.s.	n.s.	n.s.	n.s.	n.s.
guat–micr	< 0.05	< 0.05	< 0.05	< 0.05	n.s.	n.s.
guat–panu	< 0.05	n.s.	< 0.05	< 0.05	< 0.05	< 0.05
guat–poly	< 0.05	n.s.	n.s.	< 0.05	n.s.	n.s.
guat–pube	< 0.05	n.s.	< 0.05	n.s.	< 0.05	< 0.05
guat–sast	< 0.05	n.s.	< 0.05	n.s.	< 0.05	< 0.05
guat–schu	< 0.05	< 0.05	n.s.	n.s.	n.s.	< 0.05
labi–macr	< 0.05	n.s.	n.s.	n.s.	n.s.	< 0.05
labi–micr	n.s.	n.s.	n.s.	< 0.05	n.s.	< 0.05
labi–panu	< 0.05	n.s.	< 0.05	< 0.05	< 0.05	< 0.05
labi–poly	< 0.05	< 0.05	< 0.05	< 0.05	n.s.	< 0.05
labi–pube	< 0.05	< 0.05	< 0.05	n.s.	n.s.	< 0.05
labi–sast	< 0.05	n.s.	< 0.05	n.s.	n.s.	< 0.05
labi–schu	< 0.05	n.s.	n.s.	n.s.	n.s.	< 0.05
macr–micr	< 0.05	n.s.	< 0.05	n.s.	n.s.	n.s.
macr–panu	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
macr–poly	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
macr–pube	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
macr–sast	n.s.	n.s.	n.s.	n.s.	< 0.05	n.s.
macr–schu	n.s.	n.s.	n.s.	n.s.	n.s.	< 0.05
micr–panu	< 0.05	< 0.05	< 0.05	n.s.	n.s.	< 0.05
micr–poly	< 0.05	< 0.05	< 0.05	n.s.	n.s.	n.s.
micr–pube	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05
micr–sast	< 0.05	< 0.05	< 0.05	n.s.	< 0.05	< 0.05
micr–schu	< 0.05	< 0.05	< 0.05	< 0.05	n.s.	n.s.
panu–poly	n.s.	n.s.	< 0.05	< 0.05	n.s.	< 0.05
panu–pube	n.s.	n.s.	n.s.	< 0.05	< 0.05	n.s.
panu–sast	n.s.	n.s.	n.s.	n.s.	< 0.05	n.s.
panu–schu	< 0.05	n.s.	< 0.05	< 0.05	n.s.	< 0.05
poly–pube	n.s.	n.s.	< 0.05	n.s.	< 0.05	< 0.05
poly–sast	n.s.	n.s.	n.s.	n.s.	< 0.05	< 0.05
poly–schu	< 0.05	n.s.	< 0.05	< 0.05	n.s.	< 0.05
pube–sast	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
pube–schu	n.s.	n.s.	< 0.05	n.s.	< 0.05	< 0.05
sast–schu	n.s.	n.s.	< 0.05	n.s.	< 0.05	< 0.05

Appendix 3. Pairwise comparisons, respective niche overlap (Schoener's *D*) and niche similarity test *P* values. Asterisks indicate significant results ($P < 0.05$). Species names are abbreviated to the four initial letters of the specific epithet

Species pairs (a–b)	Niche overlap	Similarity a → b	Similarity b → a
cogn–croa	0.001	0.30	0.81
cogn–dens	0.000	0.44	0.38
cogn–fasc	0.376	0.04*	0.02*
cogn–guat	0.142	0.91	0.14
cogn–labi	0.284	0.71	0.53
cogn–macr	0.118	0.55	0.42
cogn–micr	0.406	0.02*	0.04*
cogn–panu	0.071	0.87	0.38
cogn–poly	0.194	0.65	0.53
cogn–pube	0.114	0.83	0.55
cogn–sast	0.000	0.24	0.32
cogn–schu	0.336	0.44	0.10
croa–dens	0.096	0.36	0.24
croa–fasc	0.000	1.23	0.36
croa–guat	0.004	0.77	0.97
croa–labi	0.000	0.75	0.59
croa–macr	0.044	0.81	0.61
croa–micr	0.000	1.11	0.87
croa–panu	0.113	0.63	0.83
croa–poly	0.047	0.46	0.85
croa–pube	0.125	0.46	0.75
croa–sast	0.480	0.06	0.08
croa–schu	0.038	0.91	0.38
dens–fasc	0.000	1.50	1.05
dens–guat	0.000	0.97	1.52
dens–labi	0.000	0.85	0.75
dens–macr	0.001	0.93	0.28
dens–micr	0.000	1.70	1.62
dens–panu	0.012	0.55	0.77
dens–poly	0.003	0.57	0.44
dens–pube	0.028	0.30	0.32
dens–sast	0.199	0.26	0.10
dens–schu	0.001	0.59	0.89
fasc–guat	0.002	0.48	0.59
fasc–labi	0.248	0.02*	0.12
fasc–macr	0.001	0.08	0.04*
fasc–micr	0.339	0.16	0.10
fasc–panu	0.000	0.18	0.93
fasc–poly	0.013	0.16	0.28
fasc–pube	0.001	0.10	0.30
fasc–sast	0.000	0.81	1.45
fasc–schu	0.022	0.48	0.42
guat–labi	0.116	0.42	0.99
guat–macr	0.163	0.08	0.69
guat–micr	0.001	0.36	0.28
guat–panu	0.101	0.20	0.73
guat–poly	0.213	0.06	0.48
guat–pube	0.106	0.79	0.65
guat–sast	0.000	0.83	0.59
guat–schu	0.474	0.02*	0.04*
labi–macr	0.048	0.24	0.18
labi–micr	0.071	0.50	0.81
labi–panu	0.025	0.42	0.89

Appendix 3. *Continued*

Species pairs (a–b)	Niche overlap	Similarity a → b	Similarity b → a
labi–poly	0.116	0.28	0.87
labi–pube	0.050	0.38	0.61
labi–sast	0.000	0.63	0.69
labi–schu	0.226	0.71	0.20
macr–micr	0.002	0.06	0.32
macr–panu	0.258	0.18	0.12
macr–poly	0.618	0.02*	0.02*
macr–pube	0.184	0.32	0.61
macr–sast	0.010	0.65	0.81
macr–schu	0.257	0.97	0.26
micr–panu	0.000	0.87	1.23
micr–poly	0.024	0.65	0.24
micr–pube	0.002	0.40	0.28
micr–sast	0.000	1.13	1.49
micr–schu	0.085	0.91	0.22
panu–poly	0.203	0.06	0.18
panu–pube	0.092	0.99	0.99
panu–sast	0.018	0.85	0.81
panu–schu	0.139	0.42	0.53
poly–pube	0.330	0.02*	0.10
poly–sast	0.013	0.48	0.50
poly–schu	0.339	0.14	0.08
pube–sast	0.067	0.38	0.32
pube–schu	0.193	0.79	0.97
sast–schu	0.011	0.57	0.59